Disintegration of *Encephalartos megastrobili*

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The female cones (megastrobili) of most *Encephalartos* species, notably *E. altensteinii* Lehm. and *E. lebomboensis* Verdoorn which were used in this study, disintegrate basipetally. Initially a decrease in the water potential of the seeds results in transfer of water from the megasporophylls to the seeds. The resulting expansion of the seeds causes an increase in the diameter of the periferal seed band which sets up a tension in the sporophyll stalks. This tension induces the autolysis of a narrow cross-sectional band of tissue in the basal part of the sporophyll stalk, followed by the rupture of the sporophyll from the cone axis at this point. The enlargement of the seeds also forces the apical seed-bearing sporophylls to slide over the sterile sporophylls at the cone apex. The subsequent dehydration of the sporophylls and simultaneous abscission of the seeds is followed much later by the abscission of the cone axis from the plant's stem to complete the disintegration process.

Die vroulike keëls (megastrobilusse) van meeste *Encephalartos*-spesies, veral *E. altensteinii* Lehm. en *E. lebomboensis* Verdoorn, disintegreer in 'n basipetale rigting. Aanvanklik verlaag die waterpotensiaal van die sade wat lei tot hul onttrekking van water uit die sporofille. Die gevolglike swelling van die sade veroorsaak 'n toename in die deursnee van die periferale saadband wat 'n spanning in die sporofilstele tot gevolg het. Hierdie spanning induseer die outolise van 'n smal dwarsliggende weefselband in die basis van die sporofilsteel waar die sporofil dan ook mettertyd van die keëlstronk losskeur. Die swelling van die sade laat die apikale saaddraende sporofille ook oor die steriele apikale sporofille gly. Die uitdroging van die sporofille en die gelyktydige afsnoering van die sade word veel later deur die afsnoering van die keëlstronk van die plant se stam opgevolg. Sodoende word die disintegreringsproses afgehandel.

Keywords: Abscission, cone disintegration, cycads, female cone, water potential

Introduction

It is common knowledge that the ripe female cones of most *Encephalartos* spp. disintegrate spontaneously, liberating the seeds which in many cases have a bright red colour (Giddy 1984). The cone axis however remains attached to the plant stem for some time, eventually withering and itself abscising from the trunk. During cone disintegration, the megasporophylls become detached from the cone axis near their bases (which is not their thinnest point) leaving a jagged unsealed scar. The detached interlocking sporophylls with seed attached, withdraw from the cone axis before breaking up further (Figure 1).

Although it is clear that the disintegration of the cones is not merely a matter of the sporophylls abscising from the cone axis and the seeds subsequently abscising from the sporophylls, no work appears to have been done on the mechanism of spontaneous female cone disintegration in the genus *Encephalartos*. This paper attempts to remedy this situation.

Materials and Methods

Female cones of *Encenhalartos altensteinii* Lehm. were used in experiments 1, 3 and 4 whilst a female cone of *E. lebomboensis* Verdoorn was used in experiment 2. After it was established that the spontaneous disintegration process is not affected by the detachment of the cones from the parent plant, most of the work was done on detached cones. They were collected a few days before disintegration commenced when other cones on the same plant or locality showed incipient signs of disintegration. The cones were kept under ordinary laboratory conditions on a bench top.

As soon as the apical seed-bearing sporophylls were found to be in the process of becoming detached from the cone axis, all the apical sporophylls which could easily be removed due to the complete or partial autolysis of a cross-sectional tissue zone near the base of the sporophyll stalk, were removed. This autolytic zone is hereafter termed an abscission zone (Raven *et al.* 1986) even though it is never accompanied by the formation of a periderm. The firmly attached central sporophylls of the cone were then used for experimental purposes and the experiments usually lasted until the basal seed-bearing sporophylls of the cone spontaneously became detached from the cone axis.

Experiment 1

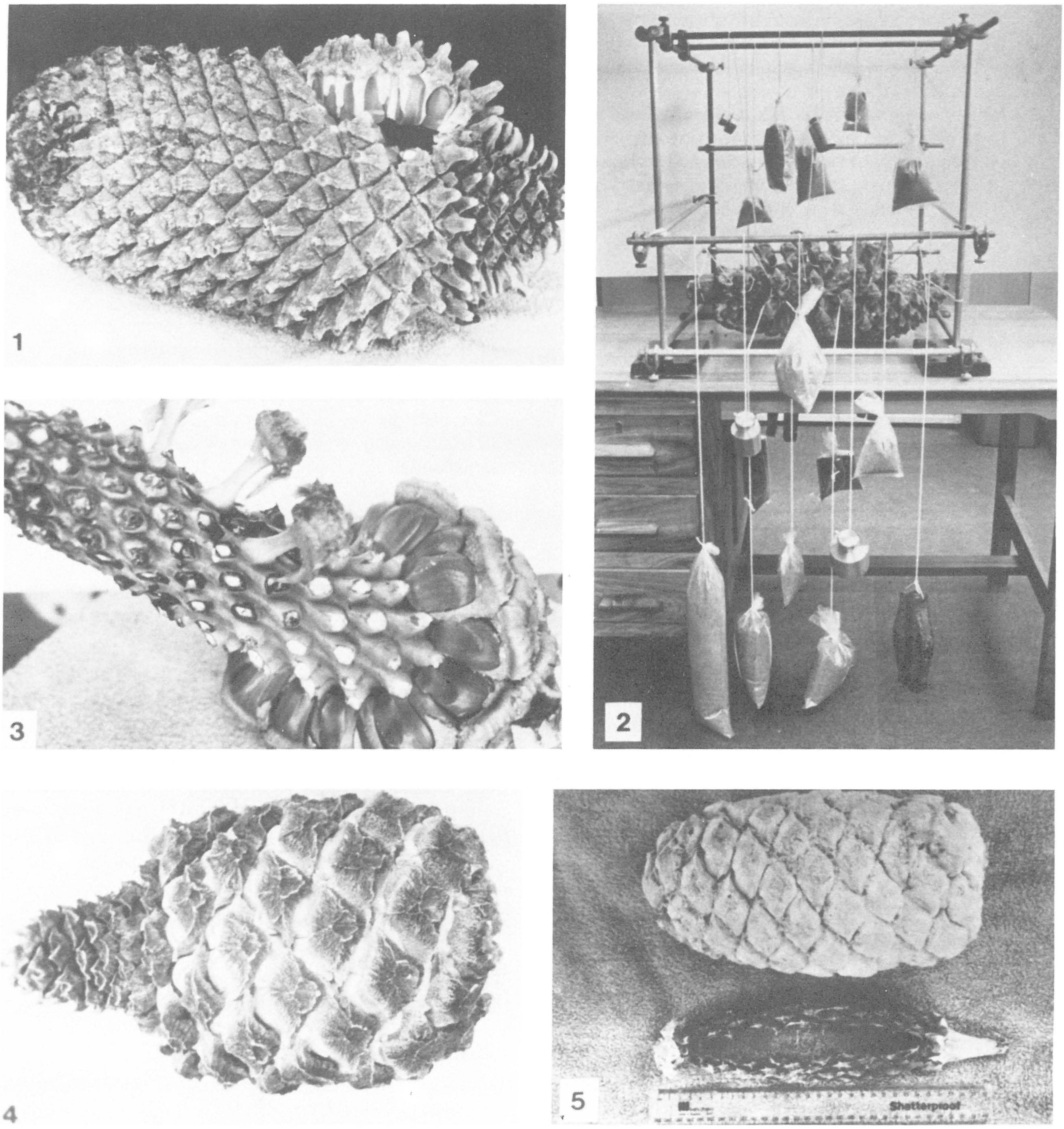
Fifty seeds were removed from sporophylls along two parastichies. The mass and the volume of the seeds was determined. Ten days later another 50 seeds were removed from two parastichies separated from the previous ones by a single parastichy of intact sporophylls. The mass and the volume of these seeds was similarly obtained.

Experiment 2

Most of the sporophylls were removed from the central part of a cone leaving five widely separated intact sporophylls. The width of the bullae of these sporophylls and the width of the seeds that were attached to them were measured on the first and tenth day by means of a vernier caliper.

Experiment 3

Sporophylls were removed daily from two adjacent parastichies equidistant from the cone apex. A 5-mm cork borer was used to remove tissue cylinders from the



Figures 1–5 **1**. Female cone of *Encephalartos altensteinii* Lehm. during early spontaneous disintegration. Apical end to right; cone 550 mm long. **2**. Female cone of *E. altensteinii* Lehm. with weights suspended from solitary sporophylls after most of the sporophylls were removed at an early stage of cone disintegration. The twine which connects the weights to the bullae of the sporophylls, pass over metal rods positioned in such a way that the force acting on the sporophylls do so in a centrifugal direction relative to the cone axis. Cone apex on right; cone 600 mm long. **3**. Female cone of *E. lebomboensis* Verdoorn, from which most sporophylls were removed at an early stage of cone disintegration. Solitary sporophylls in central part of cone did not form an abscission zone even after their seeds abscised and the mass of basal sporophylls to the right had also abscised. **4**. Mature dry female cone of *E. eugene-maraisii* Verdoorn. Cone apex left; cone length 250 mm. **5**. Mature dry female cone of *E. lanatus* Stapf & Burtt Davy above with the split axis of a similar cone below. Cone apices left; scale 300 mm long.

bullae of the sporophylls and from the sarcotestae at the micropylar end. The tissue cylinders were sliced into disks 3–4 mm thick and the sporophyll and sarcotesta disks mixed separately. Disk samples (2 g) were suspended in 50 cm^3 of 0.5, 1.0, 1.5 and 2.0 molal sucrose solutions with occasional shaking. After 1 h the disks were removed, blotted dry and reweighed. From a graphical representation of the percentage change of the disk's mass versus the water potential of the sucrose solutions, the initial water potential of the disk tissue was determined (Machlis & Torrey 1956).

Experiment 4

Most of the sporophylls were removed from the upper three quarters of a horizontally held cone in such a way that 25 widely spaced intact sporophylls remained in that region (Figure 2). The cone was securely suspended about 30 mm above a table top and weights were suspended from 20 of the solitary sporophylls by means of twine (Figure 2). The twine passed over cross bars in such a way that the forces created by the weights, acted on the sporophylls in a centrifugal direction relative to the cone axis. Five 0.2-, 0.5-, 1.0- and 2-kg weights were used. The remaining five solitary sporophylls acted as controls and did not have weights attached to them.

Each morning and evening an assessment was made of which sporophylls had detached. This was done for 14 days when the mass of sporophylls which had been left at the lower side of the cone had become completely detached from the axis.

Results

Experiment 1

During or just prior to cone disintegration the volume of the seeds increased significantly by about 10% (Table 1). Since the density of the seeds decreased slightly during this period, the volume increase is ascribed to a water-uptake process.

Experiment 2

Table 2 shows that during seed enlargement, the width of the seeds increased by 2.73% whilst the bullae of the sporophylls shrunk laterally by 8.55%. This explains why the seeds become visible during the initial stages of cone disintegration.

During this experiment it was observed that even after the mass of sporophylls at the base of the cone had become detached from the cone axis, the solitary sporophylls in the central part of the cone were still firmly attached to the cone axis. The seeds of these solitary sporophylls later abscised from the sporophylls which eventually dried out without becoming detached from the cone axis (Figure 3).

Experiment 3

It was impossible to determine the water potential of the sporophyll tissue due to the extensive excretion of mucilage by the tissue during the experiment. The sarcotesta of the seeds did however yield good results up to the stage at which the sporophylls started to abscise, at which time autolysis of the sarcotesta tissue commenced.

The water potential of the sarcotesta decreased continuously from –495 kPa to –1486 kPa during the 3 days prior to the onset of cone disintegration (Figure 6).

Experiment 4

None of the solitary sporophylls without attached weights became dislodged even after their seeds abscised and the sporophylls started to shrivel up. During this period all the sporophylls on the lower part of the cone became detached from the cone axis *en masse*.

All the solitary sporophylls from which 2-kg weights were suspended ruptured first (Figure 7). Next followed all those from which a 1-kg weight was suspended, after which only one of the sporophylls from which a 0.5-kg and 0.2-kg weight was suspended became dislodged, in that sequence. The remaining sporophylls from which 0.5- and 0.2-kg weights were suspended, like the solitary control sporophylls, remained firmly attached to the cone axis even after the sporophylls started to shrivel up.

In all cases the sporophylls that became detached from the cone axis, did so at the point at which the abscission zone normally forms and the ragged scar that was formed consisted as usual, of autolysed tissue.

Discussion

From a close inspection of disintegrating female cones of many *Encephalartos* species, it is obvious that the process is not exclusively due to the abscission of the

Table 1 Mean[1] fresh mass and volume of seeds of *Encephalartos altensteinii* Lehm. before and during cone disintegration

	Fresh mass (g)	Volume (cm^3)	Density (g cm^{-3})
Ten days before cone disintegration	9.37	8.69	1.078
During cone disintegration	10.01 (+6.83)[2]	9.56 (+10.01)[2]	1.047 (–2.88)[2]

[1]Mean of 50 seeds
[2]Percentage change

Table 2 Changes in the *in vivo* width of the megasporophyll bullae and seeds of *Encephalartos lebomboensis* Verdoorn during spontaneous cone disintegration

	Megasporophyll bullae width[1] (mm)	Seed width[1] (mm)
Before cone disintegration	38.35	23.07
Ten days later during cone disintegration	35.07 (–8.55)[2]	23.70 (+2.73)[2]

[1]Mean of 5 megasporophylls and 10 seeds
[2]Percentage change

megasporophylls from the cone axis and later the abscission of the seeds from the detached and shrivelled megasporophylls. Figure 1 shows a mass of seed-bearing sporophylls detached from the cone axis and lifted upwards in the case of a horizontally held detached cone.

The results clearly suggest that the following sequence of events describes the spontaneous disintegration of the female cones of many *Encephalartos* species: The tightly packed seeds, together with the sporophyll stalks constitute a solid periferal band a little distance from the cone axis which I hereafter will term the seed band. A few days before cone disintegration becomes evident, the water potential of the sarcotesta of the seeds starts to decrease considerably, probably as a result of the hydrolysis of macro-molecular constituents. This results in the withdrawal of water by the seeds from the sporophylls to which they are attached. The diameter of the periferal seed band increases to accomodate the collective volume increase. This sets up a tension in the sporophyll stalks which are firmly attached to the cone axis. If a sufficiently high tension is present, autolysis of a narrow cross-sectional band of tissue in the base of the sporophyll stalk occurs. The tension eventually causes the sporophyll stalk to rupture at this point leaving a ragged scar. The detached sporophylls dry out and the seeds abscise from them.

The cone axis remains attached to the plant stem for some time, eventually withering and itself abscising from the trunk to complete the disintegration of the cone.

The process described above starts at the apical end of the cone and progresses in a basipetal direction over several days. The expanding seeds also result in a lengthening of the seed band. This becomes evident during the early stages of cone disintegration by a slight acropetal movement of the apical section of the seed band over the apical sterile sporophylls which are inclined towards the cone apex. As a result of this movement, longitudinal fissures usually develop in the expanding seed band which enhances its fragmentation. The pressure exerted by the seed-bearing sporophylls on the sterile apical sporophylls also usually induces the sterile sporophylls to abscise from the cone axis.

For *E. altensteinii*, a tension in the megasporophyll stalk in excess of that created by suspending a 0.5-kg weight from the megasporophyll, usually appears to be necessary for the induction of an abscission zone in the base of the sporophyll stalk, which is not the thinnest part of the stalk.

Also, although the mature female cones of most *Encephalartos* species disintegrate spontaneously (pers. obs.), those of a few species do not. In the case of *E. dolomiticus* Lavranos & Goode, *E. dyerianus* Lavranos & Goode, *E. eugene-maraisii* Verdoorn and *E. middelburgensis* Vorster *et al.* the mature female cones simply dry out (Figure 4). During the process, the sarcotesta of the seeds do not appear to undergo autolysis. The dry cones are brittle and break up on mechanical disturbance.

In the case of *E. lanatus* Stapf & Burtt Davy, autolysis of the sarcotesta of the seeds does take place during cone maturation. However, the sporophyll stalks do not develop an abscission zone. As a consequence the tension that develops in the sporophyll stalks usually causes the cone axis to split longitudinally before the whole flattened cone eventually dries out (Figure 5). Baboons (*Papio ursinus* Kerr 1792) commonly remove the cones from the parent plants and carry them to a good vantage point. There they extract the seeds from the cones and eat the sarcotesta of the seeds, discarding the kernels.

According to Oosthuyzen [pers. comm. (Transvaal Dept. Nature Conservation, Pretoria)], the mature

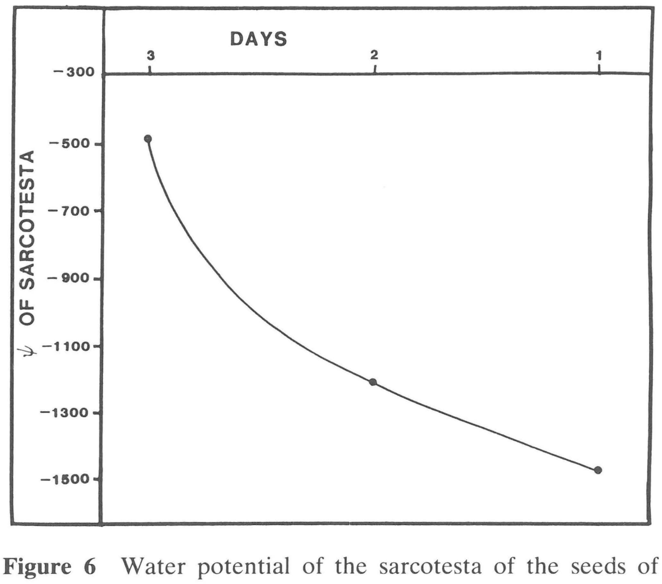


Figure 6 Water potential of the sarcotesta of the seeds of *Encephalartos altensteinii* Verdoorn, measured on different days before the visible onset of spontaneous cone disintegration.

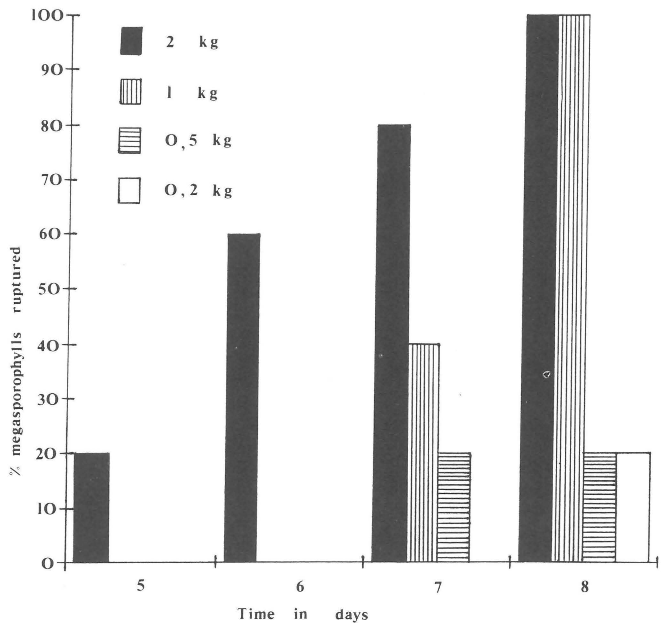


Figure 7 Time taken by various weights suspended from *Encephalartos altensteinii* Lehm. megasporophylls to induce the rupture of the sporophyll stalks.

female cones of *E. friderici-guilielmi* Lehm., *E. humilis* Verdoorn and *E. laevifolius* Stapf & Burtt Davy, also do not disintegrate spontaneously during maturation.

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